

Emergence of *Chenopodium album* and *Stellaria media* of different origins under different climatic conditions

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Summary

The emergence behaviour of weed species in relation to cultural and meteorological events was studied. Dissimilarities between populations in dormancy and germination ecology, between-year maturation conditions and seed quality and burial site climate all contribute to potentially unpredictable variability. Therefore, a weed emergence data set was produced for weed seeds of *Stellaria media* and *Chenopodium album* matured and collected from three populations (Italy, Sweden and UK). The seeds were collected in two consecutive seasons (1999 and 2000) and subsequently buried in the autumn of the same year of maturation in eight contrasting climatic locations throughout Europe and the USA. The experiment sought to explore and explain differences between the three populations in their emergence behaviour. Evidence was demonstrated of synchrony in the timing of the emergence of different populations of a species at a given burial site. The

relative magnitudes of emergence from the three populations at a given burial site in a given year were generally similar across all the burial sites in the study. The resulting data set was also used to construct a simple weed emergence model, which was tested for its application to the range of different burial environments and populations. The study demonstrated the possibility of using a simple thermal time-based model to describe part of the emergence behaviour across different burial sites, seed populations and seasons, and a simple winter chilling relationship to adjust for the magnitude of the flush of emergence at a given burial site. This study demonstrates the possibility of developing robust generic models for simple predictions of emergence timing across populations.

Keywords: predictive modelling, weed populations, winter chilling, weed seed origins, dormancy, emergence, *Chenopodium album*, *Stellaria media*, climate.

Introduction

A better understanding of the emergence behaviour of weed species in relation to cultural and meteorological events presents a number of opportunities. For example, this information could be used to target the timing of cultivation and maximize the efficacy of control strategies, regardless of whether by chemical or physical methods (Vleeshouwers, 1997). In relatively short-term studies, identification of the factors that are important in

determining the patterns of emergence for different weed species is difficult. However, when results from longer term studies are averaged over time, they often demonstrate that some weed species follow characteristic, and potentially predictable, patterns of annual emergence (Lawson *et al.*, 1974; Baskin & Baskin, 1985). The well-known periodicity tables for common agricultural weeds (Håkansson, 1982, 1983; Roberts, 1982) are derived from data averaged from such long-term emergence studies. They provide a general guide to the average

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underlying dormancy cycles and timing of emergence flushes of weed species (Roberts & Feast, 1970; Roberts & Potter, 1980; Roberts, 1982). These earlier key studies examining weed emergence were largely descriptive. Hence, although they provided a useful guide, they could not be used with different meteorological data sets in a predictive manner.

There have been significant research developments in recent years to understand and predict the emergence patterns for a number of important weed species (Grundy, 2003). The magnitude of a flush of emergence will have impact on the size and competitive pressure of a weed population, and successful prediction is likely to depend ultimately on a mechanistic understanding of dormancy (Vleeshouwers & Bouwmeester, 2001). However, the timing of the flush of emergence relative to the crop is critical in targeting and optimizing the timing of weed control (Peters, 1984; Cousens *et al.*, 1987; Berti *et al.*, 1996). Models that are capable of providing information about the timing of emergence for weed management have already been developed and are used by growers (Forcella, 1998). Currently, there may be greater scope for successfully predicting this timing of emergence rather than the magnitude, as practically applicable models for dormancy remain a challenge (Murdoch, 1998; Grundy & Mead, 2000).

Predicting the timing of emergence is becoming possible using a combination of long-term databases and relatively simple laboratory-derived models based on temperature and moisture thresholds. With a few notable exceptions, forecasting models incorporating information about weed seedling emergence have not been made available to growers or advisers. This is because a number of problems remain as bottlenecks in this research area. Several of the critical constraints and requirements to improve weed emergence models are described by Forcella *et al.* (2000), and a number of additional challenges are highlighted by Grundy (2003). Predicting the absolute magnitude of a flush of emergence is more difficult to achieve than the timing of a flush. This is because magnitude is influenced by a combination of the dormancy status, numbers, burial depth and quality of the viable seeds in the soil. Not only are the conditions for dormancy induction and loss species specific, they even vary within a species (Hartmann *et al.*, 1996). Many studies of weed dormancy and germination ecology focus on one population. One of the few exceptions to this was a study made in Scotland that looked at 18 populations of *Chenopodium album* L. (Christal *et al.*, 1998). The Scottish study demonstrated variation in the rate of dormancy relief and different temperature optima for germination among the populations examined.

Given the extent of variability described above, can generic models to predict weed emergence behaviour ever be developed or would the unexplained variability be so great that predictions would be poor and hence the challenge to produce models insurmountable? To address this question, the paper presents the results of a weed emergence experiment made by the European Weed Research Society (EWRS) working group on 'Germination and Early Growth'. The main aim of the collaborative experiment was to explore some of the challenges faced in the development of such universally applicable weed emergence models. The study produced a weed emergence data set for seeds of *C. album* and *Stellaria media* (L.) Vill., matured and collected from populations in different countries in two consecutive seasons and subsequently buried in contrasting climatic locations. These two species were chosen for the study because they were both common at the participating sites, reasonably competitive, increasingly important in organic systems and had contrasting dormancy behaviour (*C. album* has pronounced dormancy whereas *S. media* has relatively weak dormancy). Both species already feature in a number of published studies providing points of reference regarding their germination ecology. For example, *C. album* is already featured within the working predictive model WeedCast (Archer *et al.*, 2000). *Stellaria media* provided an additional challenge as it is already known to be extremely variable with numerous subpopulations having been recorded (Van der Vegte, 1978; Sobey, 1981). The resulting data set was used to explore and explain differences between the populations in their emergence behaviour and to construct a simple weed emergence model. The model was subsequently assessed for its potential application to a wide range of environments and weed populations using a series of simulated scenarios.

Materials and methods

Seeds were harvested from three well-established populations (Italy, UK and Sweden) of *C. album* and *S. media* in two consecutive years (1999 and 2000). They were harvested on warm dry days at each of the sites by shaking into paper bags to ensure that only ripe mature seeds were harvested. Seeds were then gently hand cleaned and passed through a blower to remove excess material. Precautions were made to minimize post-harvest variation in storage conditions before distribution to the eight burial sites (Italy, Germany, Sweden, Denmark, USA and three sites in the UK). Details of the three seed populations, the eight participating burial sites and burial dates are given in Table 1. In both years of the experiment, the participants at some burial sites (Denmark, Germany and USA) also included their own

Table 1 Burial site location and burial date details for the eight participating sites, stating whether seed other than the three main sources (Long Ashton-UK, Sweden, Italy) has been included in the burial experiments

Burial site	Label	Location		Burial dates		Additional local seed?
		Latitude	Longitude	1999	2000	
Morris, MN, USA	USA	45°45'N	95°53'W	22 Nov	1 Dec	Yes
Wellesbourne, UK*	Wellesbourne	52°12'N	1°36'W	10 Nov	30 Nov	No
Erlangen, Germany	Germany	49°35'N	11°02'E	8 Nov	4 Dec	Yes
Flakkebjerg, Denmark	Denmark	55°19'N	11°25'E	10 Nov	24 Nov	Yes
Uppsala, Sweden*†‡§	Sweden	59°49'N	17°39'E	31 Oct	27 Nov	No
Legnaro, Italy*†‡§	Italy	45°21'N	11°58'E	2 Nov	27 Nov	No
Long Ashton, UK†‡§	Long Ashton	51°26'N	2°40'W	4 Nov	19 Dec	No
Reading, UK	Reading	51°28'N	0°44'W	2-Nov	–	No

The seed population of *S. media* provided in 2000 from the UK was from an established population at Wellesbourne* because of insufficient numbers of this species at the Long Ashton site.

*Main seed population supplier of *S. media* in 2000.

†Main seed population supplier of *C. album* in 1999.

‡Main seed population supplier of *S. media* in 1999.

§Main seed population supplier of *C. album* in 2000.

local seed populations of the two study species for comparison (Table 1). The inclusion of these local seed populations was not a compulsory activity of the collaborative study; however, it provided valuable emergence data for additional populations.

Four replicates of each of the three populations were assessed at each site. For sites where four populations (the three common populations plus a local population) were included, treatments were arranged according to a Latin square design (four rows by four columns). Where only three populations were included, treatments were arranged according to an incomplete Latin square (three rows by four columns). When data for the three populations were analysed across burial sites, these blocking structures could not easily be included and so, for these analyses, the design within each site was assumed to be a randomized complete block design.

In November 1999, 12 pots (or 16 pots if a local seed population was included) were buried in the ground at each of the eight burial sites so that the inner rim of the pots was level with the surrounding ground. These pots were 19 cm diameter at the base, 22.6 cm high and 26.5 cm diameter at the top. Fine nylon crinalin mesh (Whalleys, Bradford, UK) was fixed to the inside of the bottom of the pots to deter worms from entering the pots. A total of 500 seeds of *S. media* and 500 seeds of *C. album* were buried in each pot at a depth of 1 cm, separate pots being used for each of the three seed populations. A standard substrate was used at all the participating burial sites supplied by Kekkila Finnpeat, Finland, except in the USA, where local products were used to reconstruct the substrate used in Europe. The substrate was a medium to coarse peat with added dolomitic limestone to achieve a pH of 5.5. The substrate was sieved to eliminate pieces of wood and humidified with 10 L of deionized water for every 27 kg

of substrate. To reduce site-to-site experimental differences in compaction, successive layers (5–7 cm) of sieved and humidified substrate were added to each pot and compacted using a 10-kg weight (each time equally distributed over the surface of the substrate) before the addition of the next layer. The inner rim of the pot was used as a guide to ensure that seeds were buried at a uniform depth of 1 cm at all sites. The final level of substrate in the buried pots was level with the surrounding ground. The pots were finally humidified by slowly adding 300 mL of deionized water per pot, and a further 300 mL was added after 6 h and again after 12 h (total of ≈ 1 L per pot). Stainless steel wire netting made from 21 standard gauge wire (equivalent of 0.8 mm) and giving a 6 mm \times 6 mm square hole was fixed to the top of each pot. This was a small enough gauge to prevent small rodents (and birds) from entering while keeping any shading effect it may have had on light interception to a minimum.

Daily precipitation and maximum and minimum air temperatures were collected at each site throughout the study. In addition, maximum and minimum soil temperatures were recorded at seed burial depth using small data loggers. Numbers of emerged weed seedlings were recorded and then removed by cutting seedling stems at ground level with minimum disturbance of the substrate. Seedling emergence was recorded on at least a weekly basis during the active periods of emergence in spring and autumn. At all eight locations, the emergence was monitored for a minimum of 12 months and, at the majority of sites, additional data were obtained for a second year of burial.

In November 2000, the experiment was repeated using the same experimental protocol, but using 1000 seeds of both species from UK and Italy in each pot. For the Swedish seed harvested in 2000, there were only

sufficient quantities for 500 seeds of *S. media* per pot and 800 seeds of *C. album* per pot. The *S. media* provided by the UK in 2000 was harvested at the Wellesbourne site, because of low seed numbers from the original Long Ashton population that had been used in 1999 (Table 1).

Comparison of weather between burial sites

Various summaries (total rainfall, proportion of wet days, minimum, maximum and average air temperature, and proportions of days with minimum or maximum temperature below 0 °C) of the meteorological data were calculated for each month at each site over the 2-year period.

Relative magnitude of emergence responses

To study the effects of both study population and burial site on the magnitude of emergence, total emergence counts of each species from each pot on each site were calculated for each full calendar year from the time of burial (i.e. November 1999–October 2000 and November 2000–October 2001 for the 1999 sowing, and November 2000–October 2001 for the 2000 sowing). These total emergence counts were expressed as percentages of the number of seeds sown and, after arcsine transformation, subjected to analysis of variance. A combined analysis was performed for the emergence counts in each time period, for each species across all burial sites (as appropriate) for the three populations, assuming a randomized complete block design within each site. Main effects of the differences between burial sites were assessed relative to the pooled between-block (replicate) residual mean square, with the main effect of seed population and the interaction between burial site and seed population assessed relative to the pooled within-block (replicate) residual mean square. For those sites (Denmark, Germany and USA) where an additional local seed population was included, a separate and additional within-site analysis was also performed for each variable for each species.

Relationship between emergence magnitude and weather

Initial examination of the emergence data for *C. album* suggested that the magnitude of response at a site might be related to the depth of chilling at the site. The magnitude of response for the first year of each sowing was plotted against meteorological variables. A formal analysis of possible relationships was obtained by regressing the total emergence counts as a proportion of the number of seeds sown against each meteorological summary variable using logistic regression (a generalized

linear model assuming a binomial error structure and logit link function; Lane & Payne, 2000). This approach was used in preference to linear regression to ensure that predicted proportions could not be less than zero. For each meteorological variable, four models were assessed – a single line for both years, parallel lines with intercept varying between years, coincident lines with slope varying between years, and separate lines with both slope and intercept varying between years.

Relative timing of emergence responses

To examine the effect of weed population and burial site on the relative timing of emergence, cumulative emergence counts were plotted against time for each weed population at each site. A simple model to describe the cumulative emergence counts for *S. media* was then developed based on the approach used in WeedCast (Archer *et al.*, 2000). The data for the Danish local seed population sown in Denmark in 1999 were chosen to develop this simple thermal model. This burial site and seed population was chosen because the data at this burial site were complete and recorded regularly and, importantly, the magnitude of emergence for this population had been particularly high, providing a substantial number of seedling observations on which to base a model. These criteria are essential for robust model development. Working with the cumulative emergence counts summed across replicates, a Gompertz function with a lower asymptote of zero was used to describe the relationship between cumulative emergence and accumulated thermal time. The most appropriate base temperature (which was found to be 2 °C to the nearest whole degree) was estimated by fitting the Gompertz function against each of the thermal time variables and selecting that which gave the minimum residual mean square, using the non-linear curve-fitting facilities in GENSTAT for Windows (Lane & Payne, 2000). Thermal time was expressed in terms of day-degrees above the base temperature. These calculations were performed using the HEATUNITS procedure (Reader *et al.*, 2000) in GENSTAT for Windows from the observed minimum and maximum daily air temperatures. The fitted emergence response was then re-expressed relative to calendar time, and lack-of-fit of the response was compared with the patterns of daily rainfall.

The general applicability of this simple model for emergence timing, developed for a local weed population at one burial site, was then assessed against three hypotheses – that it could be used to predict the emergence response:

- 1 for different (alien) weed populations at the same burial site;

- 2 for a single weed population at a range of different burial sites; and
- 3 for local weed populations in a different calendar year.

These hypotheses were assessed visually by plotting the observed and predicted cumulative emergence counts against calendar time for the appropriate combinations of study population, burial site and year. Predicted cumulative emergence counts were calculated using the fitted parameters from the Danish local seed population, with the upper asymptote parameter scaled according to the total observed emergence over the calendar year, and the appropriate local meteorological data.

Results

Differences in meteorological data at the participating sites

The pattern of average monthly temperature showed an expected similarity between burial sites (Fig. 1A); however, the differences between the European burial sites in any given month were up to 10 °C. Notably, the USA monthly average during the winter months was significantly lower than any of the European burial sites. The frequency of days when the temperature dropped below freezing at some point during the day (Fig. 1B) also showed a similar pattern among burial sites. In the winter of 1999/2000, the burial sites could be classified into two groups. First, Germany, Italy, Sweden and the USA, where the temperature dropped below freezing on more than 50% of days between November and February. Secondly, the remaining sites (Denmark and the three UK sites) with fewer freezing days. However, for the winter of 2000/2001, the distinction between these groups is less clear; the Italian winter was notably warmer and the Danish one colder than the previous winter. The UK burial sites were generally wetter with erratic wetting events at some of the other European burial sites, whereas the apparently 'dry' winter conditions in the USA were the result of its mid-continental position (Fig. 1C).

Relative magnitude of emergence responses

Highly significant effects ($P < 0.001$) of seed population and burial site were observed for percentage weed emergence for *C. album* and *S. media* in both years of the study. There appeared to be a similar relative emergence response for seed produced in both 1999 and 2000 in both their first and second years of burial (Fig. 2A). The USA burial site always had the highest

emergence and, generally, the UK burial sites the lowest emergence. For the *C. album* matured in 1999, the UK seed population always had significantly greater emergence than the Swedish seed population, and the Swedish seed population showed significantly greater emergence than the Italian seed population ($P < 0.001$; Fig. 2B). However, from the seed matured during 2000, the Italian seed population had significantly better emergence than both the other populations ($P < 0.001$). Interactions were also observed. For example, the seed population from the UK buried in Sweden in 1999 had relatively high emergence compared with the other two seed populations at that burial site (Table 2A). In the second year of burial, for the seed populations buried in 1999, the emergence response at the USA burial site was unusually high for the seed population from the UK (Table 2B). For the seed buried in 2000, despite the relatively high emergence of the Italian seed population noted previously, this effect was notably absent at the Swedish burial site (Table 2C). Considering the emergence behaviour of the local seed populations relative to that of the three common seed populations, the Danish and German local seed populations had responses that were similar to those of the Swedish and UK seed populations respectively (Table 2). However, there was little similarity between the responses for the local USA seed population and those for any of the European seed populations.

There appeared to be a relationship between the climatic conditions at each of the burial sites and the relative magnitude of the flush of emergence of *C. album* (regardless of seed population, burial year or seed maturation year). The percentage emergence at each burial site in a 12-month period was plotted against the mean winter temperature at that site. An apparent inverse relationship indicated that the lower the mean winter temperature, the greater the magnitude of the flush of emergence in the first year after burial (Fig. 3). The slope of the fitted logistic relationship appeared to be different for the two successive burial years, with a steeper response in 1999.

The response for *S. media* was more complex, and there were no consistent trends evident between years or among burial sites (Fig. 4A). One notable observation, as observed for *C. album*, was that the Italian seed population harvested in 2000 gave significantly greater emergence than all the other main seed populations of *S. media* across all burial sites ($P < 0.001$; Fig. 4B).

For the seed populations buried in 1999, although the pattern seen at each burial site was similar to that observed overall (Fig. 4B), the local seed populations

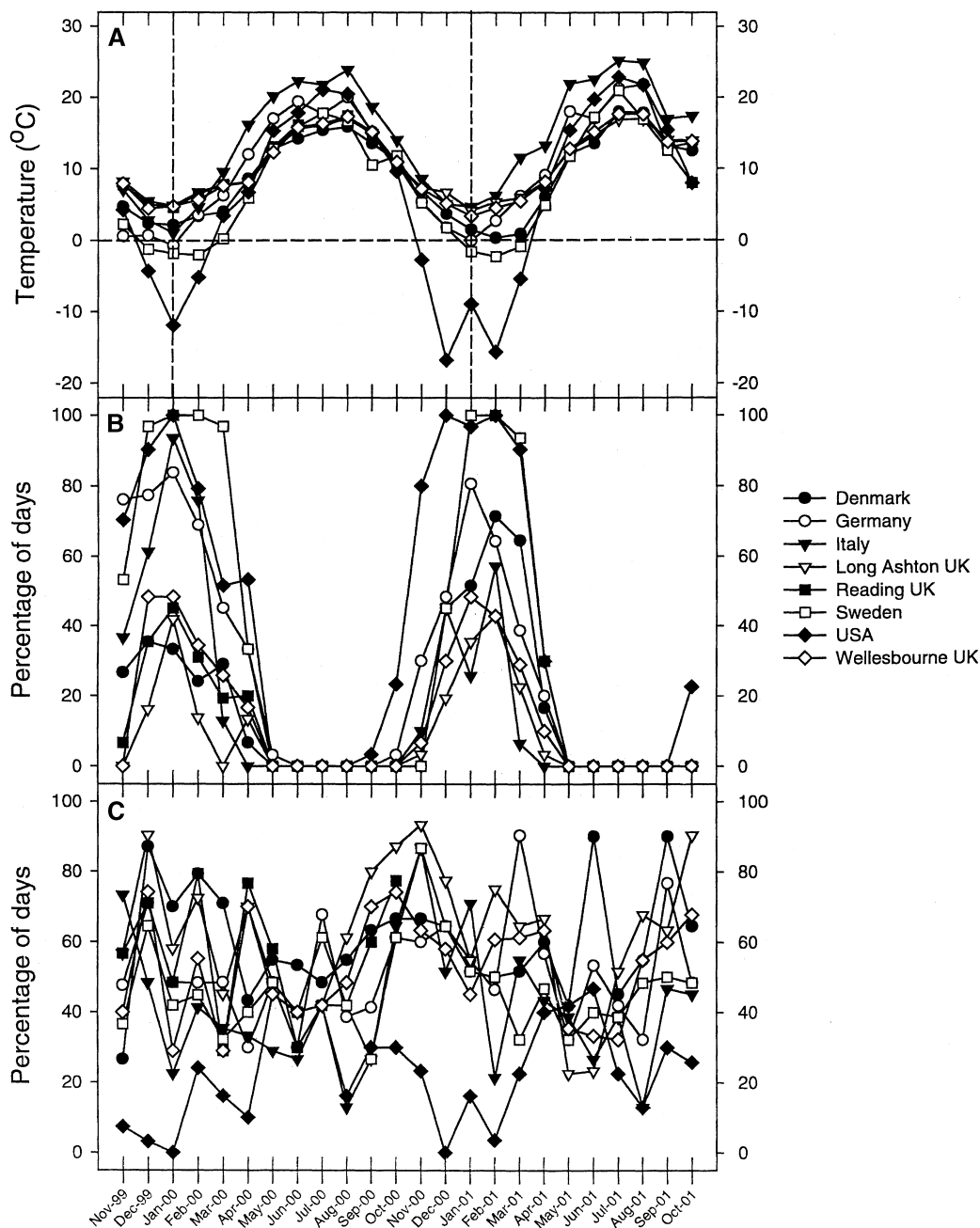


Fig. 1 Summary of meteorological records for the eight burial sites over the two years of study: (A) average monthly temperature (°C); (B) percentage of days with minimum temperature < 0 °C; (C) percentage of days with rainfall. Vertical dashed lines indicate January of each year; horizontal dashed line indicates an average monthly temperature of zero.

(i.e. Swedish seed buried in Sweden, Italian seed buried in Italy and UK-Long Ashton seed buried in Long Ashton) had a higher response than expected (Table 3A). In the second year of burial for the 1999 seed, the response was generally low, except for the UK and Italian seed populations in Denmark and the Swedish and Italian seed populations in the UK (Table 3B). For the seed populations buried in 2000, although the Italian seed population was generally

observed to give a statistically significantly higher overall emergence response, this was not the case at the burial sites in Denmark or Sweden (Table 3C).

Considering the emergence behaviour of the additional local seed populations relative to that of the three common seed populations, the Danish local population had responses that were similar to those of the Swedish seed population (Table 3). Again, however, there was little consistent similarity between the responses for the

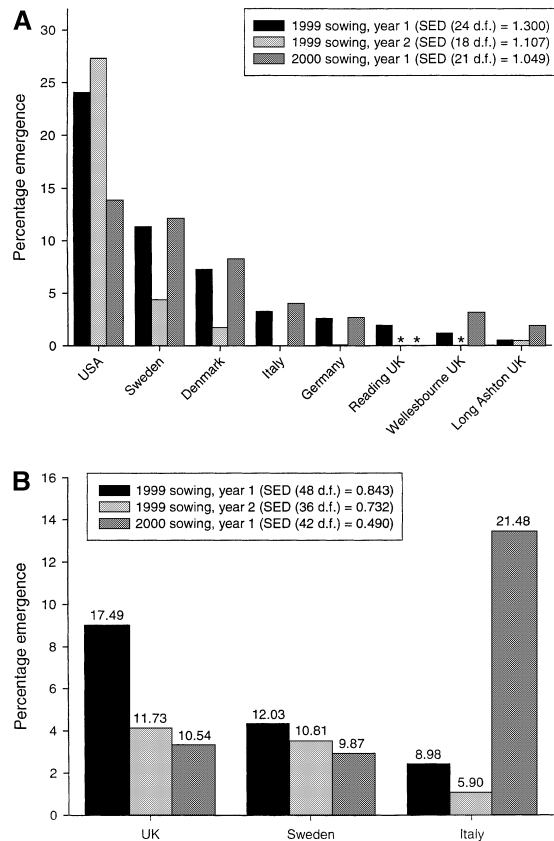


Fig. 2 Total emergence of *Chenopodium album* between November 1999 and October 2000 inclusive as a percentage of the number of seeds sown in November 1999 (1999 sowing, year 1); between November 2000 and October 2001 inclusive as a percentage of the number of seeds sown in November 1999 (1999 sowing, year 2); between November 2000 and October 2001 inclusive as a percentage of the number of seeds sown in November 2000 (2000 sowing, year 1). (A) Mean values for each burial site, averaged across the three main seed populations, ordered by values (1999 sowing, year 1); (B) mean values for each weed population, averaged across the eight burial sites. Angle-transformed values shown above each bar together with appropriate SEDs on this scale. Data sets marked with * were not collected.

USA local seed population and those for any of the European seed populations.

Relative timing of emergence responses

At any given burial site, the timing of the flushes of emergence was generally consistent among the study populations. The simple thermal model fitted the cumulative emergence data for Danish *S. media* seed buried in Denmark (in November 1999) reasonably well; however, there appeared to be a lack of fit at approximately 500 accumulated day-degrees above a base of 2 °C (Fig. 5A). After the model results, along with the observed emergence data, had been plotted using the calendar scale, rather than the day-degree scale

(Fig. 5B), the lack of fit was seen to coincide with a period lacking precipitation (Fig. 5C).

Scenario 1: different seed populations at the same burial site

The first scenario, using the simple thermal model, tested the possibility of predicting the timing of *S. media* emergence in the same first year of burial for the three main weed populations (UK, Italy and Sweden) at the Danish burial site. Encouragingly, some synchrony occurred in the timing of emergence for all four seed populations of *S. media* at the Danish site. The model predicted the observed data reasonably well for the three non-local populations (Fig. 6). The lack-of-fit alluded to earlier during the dry period was also seen for the UK and, in particular, the Italian seed population. Notably, the model appeared to fit cumulative emergence from the Sweden seed population in Denmark very well.

Scenario 2: the same seed population buried at different burial sites

The simple thermal model gave a good description of the emergence behaviour of the Swedish seed population in Denmark. Therefore, as the model appeared to be acceptable for this seed population, it was extended to describe the behaviour of the same population of *S. media* in Sweden; however, it predicted that the start of the emergence flush would be slightly later than was actually observed (Fig. 7A). The same was seen for the emergence behaviour of the Swedish seed population in the USA, with the model being slightly too slow to predict the start of the flush of emergence (Fig. 7B). The major spring flush in Germany was also predicted reasonably well (Fig. 7C). In contrast, the model predictions for the emergence behaviour of the Swedish seed population buried in Italy and the UK agreed poorly with what was observed at these burial sites. For example, at the Italian burial site, although the model predicted the very small spring flush, it completely missed the first (1999) and second (2000) autumn flushes (Fig. 7D). The model predictions were poor for the emergence behaviour of the Swedish seed population at all three UK burial sites. In all three cases, the model completely failed to predict the first autumn flush (1999) and gave a premature prediction of the 2000 spring flush (Fig. 7E–G). The magnitude of the response at the Long Ashton burial site was very small, with no obvious spring flush occurring and a small mid-summer flush of approximately 20 seedlings summed over all pots (Fig. 7G).

Table 2 Total emergence of *Chenopodium album*: (A) between November 1999 and October 2000 inclusive, given as a percentage of the number of seeds sown in November 1999; (B) between November 2000 and October 2001 inclusive, given as a percentage of the number of seeds sown in November 1999; (C) between November 2000 and October 2001 inclusive, given as a percentage of the number of seeds sown in November 2000. Angle-transformed means shown in parentheses alongside back-transformed percentages

(A) Site	Seed population			
	UK	Sweden	Italy	Local
USA	29.5 (32.92)	23.6 (29.05)	19.5 (26.17)	18.0 (25.06)
Wellesbourne UK	1.8 (7.81)	2.3 (8.67)	0.1 (2.19)	–
Germany	6.4 (14.61)	2.9 (9.74)	0.4 (3.45)	2.3 (8.70)
Denmark	14.0 (21.96)	5.4 (13.49)	3.9 (11.42)	16.4 (23.89)
Sweden	30.9 (33.75)	8.2 (16.62)	2.3 (8.71)	–
Italy	4.4 (12.15)	3.2 (10.24)	2.3 (8.78)	–
Long Ashton UK	1.3 (6.64)	0.3 (3.30)	0.2 (2.39)	–
Reading UK	3.1 (10.06)	0.8 (5.17)	2.3 (8.76)	–

SED (48 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 2.341; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 2.384; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 1.958 (USA local seed population), 1.203 (German local seed population) and 2.230 (Danish local seed population).

(B) Site	Seed population			
	UK	Sweden	Italy	Local
USA	50.7 (45.40)	27.3 (31.50)	9.2 (17.70)	41.5 (40.09)
Germany	0.1 (1.55)	0.1 (2.19)	0.0 (1.28)	0.9 (5.46)
Denmark	1.1 (5.91)	3.8 (11.22)	0.9 (5.46)	1.2 (6.04)
Sweden	4.6 (12.37)	7.3 (15.70)	2.0 (8.11)	–
Italy	0.0 (0.00)	0.0 (0.64)	0.0 (0.00)	–
Long Ashton UK	0.8 (5.18)	0.4 (3.62)	0.2 (2.86)	–

SED (36 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 1.836; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 1.793; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 2.737 (USA local seed population), 1.132 (German local seed population) and 1.094 (Danish local seed population).

(C) Site	Seed population			
	UK	Sweden	Italy	Local
USA	8.4 (16.86)	7.6 (16.02)	29.2 (32.73)	15.7 (23.32)
Wellesbourne UK	1.2 (6.34)	0.4 (3.81)	12.1 (20.36)	–
Germany	0.9 (5.54)	0.8 (5.10)	8.9 (17.36)	1.1 (6.06)
Denmark	3.5 (10.74)	8.1 (16.51)	15.0 (22.8)	9.6 (18.06)
Sweden	13.7 (21.69)	9.3 (17.71)	13.8 (21.77)	–
Italy	1.9 (7.90)	1.6 (7.20)	11.0 (19.33)	–
Long Ashton UK	0.7 (4.70)	0.2 (2.74)	7.6 (16.01)	–

SED (42 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 1.490; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 1.296; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 1.284 (USA local seed population), 0.959 (German local seed population) and 1.161 (Danish local seed population).

Scenario 3: the same seed population and same burial site but seed matured in different seasons

The model developed using the Danish local seed population of *S. media*, matured and buried in 1999, was used to predict the emergence behaviour of the same Danish local seed population (matured and buried in 1999) during 2000/2001 at the Danish burial site (Fig. 8A). It was also used to predict the emergence

behaviour of another Danish local seed population (matured and buried in 2000) during 2000/2001 at the Danish burial site (Fig. 8B). The main (spring) flush for the 1999-buried seed in its second year of burial was predicted well (Fig. 8A), as was that for the 2000-buried seed (Fig. 8B). However, the model failed to predict the autumn 2000 flush for the latter population (Fig. 8B).

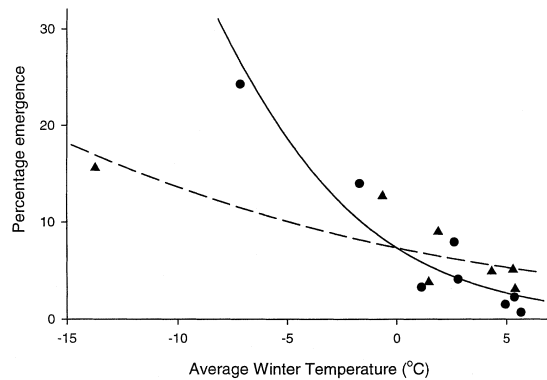


Fig. 3 Relationship between the magnitude of emergence of *Chenopodium albus* and the level of winter chilling, as given by the average temperature (°C) during the December, January and February preceding the spring flush. (A) 1999 sowing, year 1: filled circles, observed burial site means; solid line, fitted logistic regression. (B) 2000 sowing, year 1: filled triangles, observed burial site means; dashed line, fitted logistic regression.

Discussion

The seed populations used for the study were selected specifically to obtain seeds that originated from established populations with different climates and maturation conditions. Initial observations of the consistency in the timing of the major flushes of emergence between the weed populations have been encouraging. They suggest that there is some synchrony in the initiation of germination that is not significantly affected by seed population, given the limited number of populations in the present study. The observed differences in the proportion of emerged seedlings from the different seed populations were generally consistent across burial sites. This suggested that there were differences in the initial viability or dormancy status of these seed populations, reflected in their relative emergence responses, regardless of the environment in which they were then buried. The most significant, and potentially difficult to predict, differences were in these respective magnitudes of the flushes of emergence between the weed populations at any given site. These between-population differences are also likely to vary between seasons depending on maturation conditions in a given year (Hartmann *et al.*, 1996; Sharif-Zadeh & Murdoch, 2000). For example, was there something in the maturation conditions during 2000 in Italy that produced seed of lower dormancy and hence greater emergence? If so, might examination of the 2000 meteorological records for the Italian site identify these conditions? The results from studies such as the present experiment may allow these complex interactions between maturation and burial environment to be highlighted and potentially quantified. One factor might be the accumulated fraction of active phytochrome B during drying in sunlight, enabling seeds to germinate in

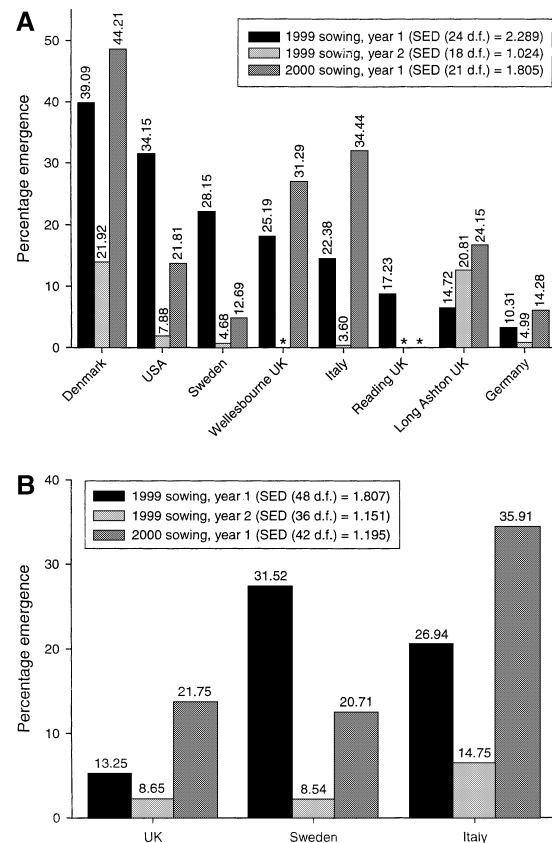


Fig. 4 Total emergence of *Stellaria media* between November 1999 and October 2000 (inclusive), given as a percentage of the number of seeds sown in November 1999 (1999 sowing, year 1); the same between November 2000 and October 2001 (inclusive) given as a percentage of the number of seeds sown in November 1999 (1999 sowing, year 2); the same between November 2000 and October 2001 (inclusive) given as a percentage of the number of seeds sown in November 2000 (2000 sowing, year 1). (A) Mean values for each burial site, averaged across the three main seed populations, ordered by values (1999 sowing, year 1). (B) Mean values for each main seed population, averaged across the eight burial sites. Angle-transformed values shown above each bar together with appropriate SEDs on this scale. Data sets marked with * were not collected.

darkness for an extended period (Kendrick, 1976; Hartmann *et al.*, 1997). The study also raises questions about the interaction between genotype and environment. Where an additional local seed population was included, at two burial sites (Denmark, Germany), the magnitude of the emergence response for the local population was similar to one of the common populations. However, for the USA burial site, any agreement between the USA local seed population and any of the European seed populations was difficult to establish. Possibly, the environment at the USA burial site was so different from that at any of the European sites that none of the non-local populations had consistently the right characteristics to adjust to the local environment as well as the local USA seed population.

Table 3 Total emergence of *Stellaria media*: (A) between November 1999 and October 2000 inclusive, given as a percentage of the number of seeds sown in November 1999; (B) between November 2000 and October 2001 inclusive, given as a percentage of the number of seeds sown in November 1999; (C) between November 2000 and October 2001 inclusive, given as a percentage of the number of seeds sown in November 2000. Angle-transformed means shown in parentheses alongside back-transformed percentages

(A) Site	Seed population			
	UK	Sweden	Italy	Local
USA	12.5 (20.71)	47.6 (43.61)	38.1 (38.12)	43.9 (41.5)
Wellesbourne UK	3.1 (10.22)	31.0 (33.83)	27.3 (31.52)	–
Germany	0.7 (4.78)	6.6 (14.88)	3.8 (11.29)	–
Denmark	10.3 (18.68)	66.1 (54.40)	48.6 (44.20)	82.3 (65.13)
Sweden	8.2 (16.60)	47.3 (43.44)	17.1 (24.41)	–
Italy	3.2 (10.24)	22.7 (28.45)	22.7 (28.45)	–
Long Ashton UK	4.9 (12.85)	4.4 (12.17)	10.8 (19.15)	–
Reading UK	4.3 (11.90)	13.3 (21.41)	9.9 (18.38)	–

SED (48 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 4.759; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 5.110; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 4.05 (USA local seed population) and 1.580 (Danish local seed population).

(B) Site	Seed population			
	UK	Sweden	Italy	Local
USA	3.0 (9.91)	0.7 (4.77)	2.4 (8.96)	4.9 (12.77)
Germany	0.1 (1.55)	0.6 (4.40)	2.5 (9.03)	–
Denmark	20.8 (27.12)	1.9 (8.02)	25.9 (30.61)	3.7 (11.1)
Sweden	0.4 (3.47)	1.0 (5.69)	0.7 (4.89)	–
Italy	0.2 (2.66)	0.3 (2.98)	0.8 (5.17)	–
Long Ashton UK	1.6 (7.20)	18.4 (25.39)	24.8 (29.84)	–

SED (36 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 2.520; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 2.820; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 1.602 (USA local seed population) and 3.17 (Danish local seed population).

(C) Site	Seed population			
	UK	Sweden	Italy	Local
USA	7.5 (15.87)	8.0 (16.38)	30.0 (33.19)	19.1 (25.94)
Wellesbourne UK	16.4 (23.90)	15.8 (23.42)	52.7 (46.55)	–
Germany	2.5 (9.16)	1.5 (7.07)	20.0 (26.59)	6.2 (14.44)
Denmark	46.2 (42.80)	46.2 (42.80)	53.5 (47.02)	54.5 (47.6)
Sweden	3.8 (11.17)	6.5 (14.76)	4.4 (12.13)	–
Italy	25.8 (30.50)	15.2 (22.94)	58.5 (49.89)	–
Long Ashton UK	10.4 (18.86)	9.1 (17.56)	34.6 (36.02)	–

SED (42 d.f.) for comparing means from the same seed populations (from UK, Sweden and Italy only) = 3.151; SED for comparing means at the same burial site for the seed populations from the UK, Sweden and Italy only = 3.163; SED (9 d.f.) for comparing means from local seed populations with the three main seed populations at specified burial sites = 2.374 (USA local seed population), 4.288 (German local seed population) and 4.11 (Danish local seed population).

Interestingly, a simple correlation exists between the severity of the winter and the relative magnitude of the flush of emergence for *C. album* observed across all burial sites and seed populations. Importantly, the use of mean winter temperature as the explanatory variable in the present study may not have been the best or only choice. The relationship presented is simply to illustrate the principle that it may be possible to provide some way of 'scaling' the magnitude of a flush of emergence

for this species from burial site to burial site. Other more suitable variables may include the cumulated time spent below some critical temperature greater than 0 °C. For *C. album*, however, there does appear to be a simple correlation with the depth and length of winter temperature. Burial sites with lower winter temperatures could be more conducive to preserving greater numbers of seeds over the winter months, which subsequently become available for germination as the soil warms in

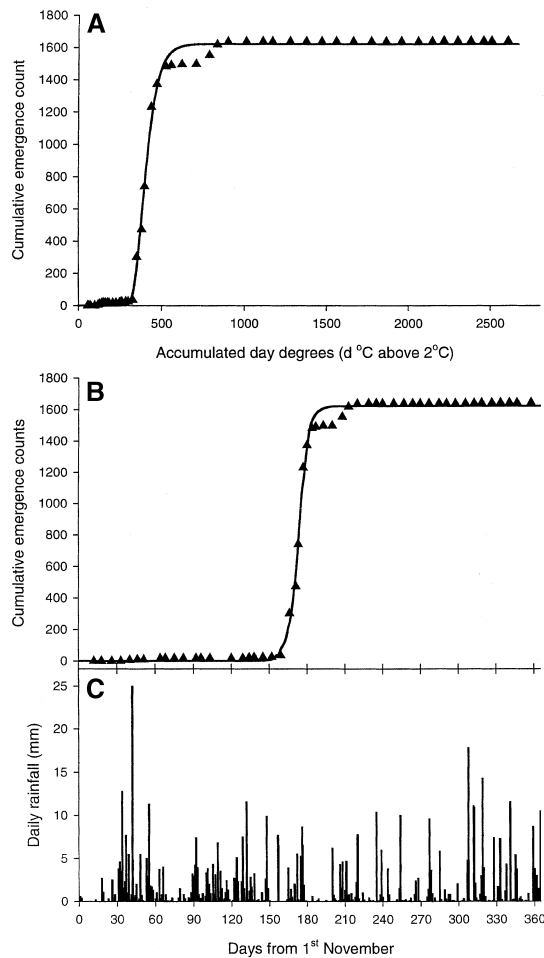


Fig. 5 Fitting the emergence timing model for the Danish local seed population of *Stellaria media* buried in Denmark in November 1999. Cumulative emergence counts between November 1999 and October 2000 inclusive. (A) Cumulative emergence counts against accumulated day-degrees above 2 °C. (B) Cumulative emergence counts against day number. (C) Daily rainfall. For (A) and (B): filled triangles, observed cumulative emergence counts; solid line, fitted cumulative emergence counts.

the spring. The relationship identified in this study for *C. album* may be due to its pronounced dormancy (Murdoch & Ellis, 2000), which thus makes it more likely to be able to identify and find a relationship between a dormancy-breaking meteorological variable and the subsequent magnitude of emergence. For example, a deeper winter chilling may have a greater dormancy-breaking effect than a relatively mild winter chill, hence releasing a greater proportion of the population to be available for germination. Only by identifying these differences in studies such as this can we hope to go on to understand what factors are important in causing variability and hence allow for this in future models.

The observations for *S. media* were more difficult to generalize. Dormancy is much less pronounced in *S. media*, hence the less distinguishable patterns in

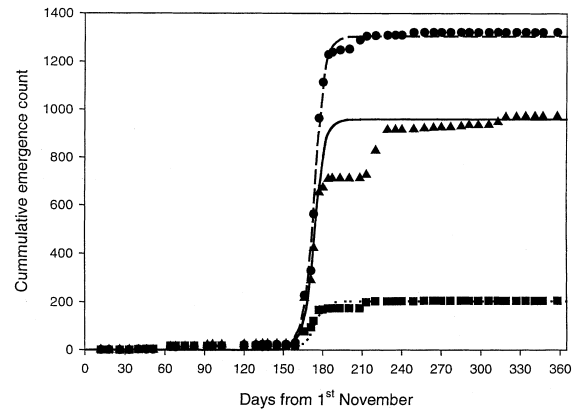


Fig. 6 Observed and predicted emergence timing for non-local seed populations of *Stellaria media* buried in Denmark in November 1999. Cumulative emergence counts between November 1999 and October 2000 inclusive. [UK seed population (dotted line, predicted emergence; filled squares, observed emergence); Italian seed population (solid line, predicted emergence; filled triangles, observed emergence); Swedish seed population (dashed line, predicted emergence; filled circles, observed cumulative emergence counts).]

magnitude may have been more attributable to direct responses to prevailing weather conditions than to any predetermined (potentially dormancy-related) pattern induced during the winter months. A more complex interaction between the maternal ripening environment and the burial environment was also likely, but this cannot be explained at present.

The synchrony between the timing of at least the spring flush of emergence of all seed populations at a given burial site suggests the potential for finding suitable models eventually to predict the timing of emergence for multiple populations. A simple thermal model as presented here, with the addition of a moisture threshold, may therefore improve the fit of the model and provide a more appropriate approach. Importantly, the point at which thermal time starts to accumulate will have a huge impact on the predicted timing of emergence for these models. When fitting the model to an observed data set, time zero can be defined to be any time before the start of emergence without affecting how well the model fits the observed data. However, to predict emergence correctly in a different environment, identification of a meaningful, biological event from which temperature accumulation should start is essential. This is almost certainly associated with a significant dormancy-breaking process. One such example is that given by Bouwmeester & Karssen (1993), who developed a temperature-based model for germination of *C. album* that incorporated a dependency on dormancy induction and relief events.

The continual failure of the simple model to detect the autumn flushes of emergence is notable. Perhaps this observation was related to the mildness of the autumn

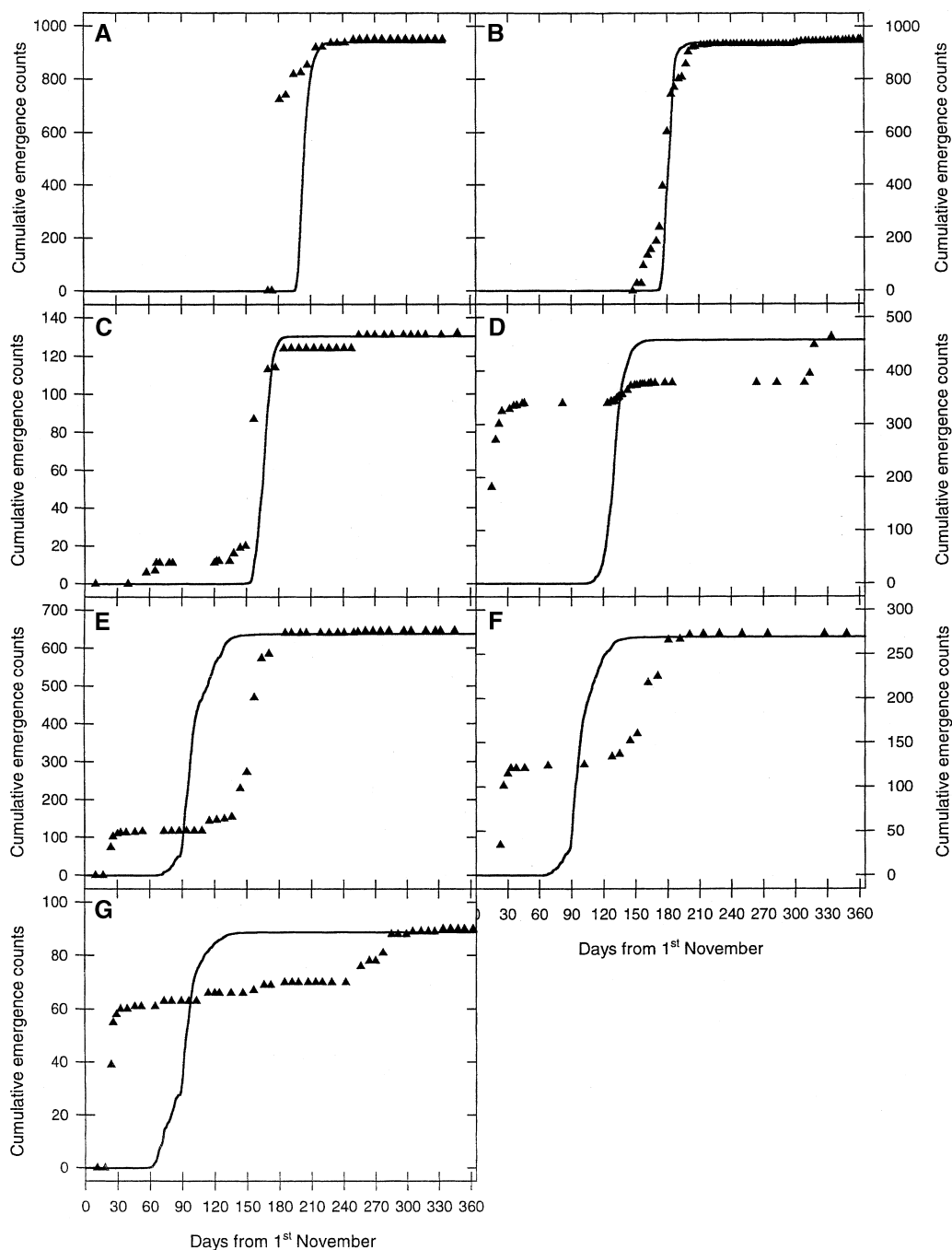


Fig. 7 Observed and predicted emergence timing for the Swedish seed population of *Stellaria media* buried at various burial sites in November 1999. Cumulative emergence counts between November 1999 and October 2000 inclusive: (A) Sweden; (B) USA; (C) Germany; (D) Italy; (E) Wellesbourne; (F) Reading; (G) Long Ashton; filled triangles, observed cumulative emergence counts; solid line, predicted cumulative emergence counts. Note different scales for cumulative emergence counts.

weather conditions at some but not all burial sites (e.g. Italy and the UK) and the fact that the model was constructed from data where an autumn flush was not observed (Denmark in 1999). An adjustment factor that could allow for latitude, day length or continental position/coastal proximity or soil moisture could improve model predictions of emergence at different burial sites.

To alleviate restrictions with distribution of soil to the different participating burial sites, a standard peat-based substrate was used. However, the peat, although providing a solution to this particular problem, also created problems associated with its insulating properties, the different way in which it wetted and dried compared with mineral soil and its proclivity to heave and sometimes crack. Differences between the cracking

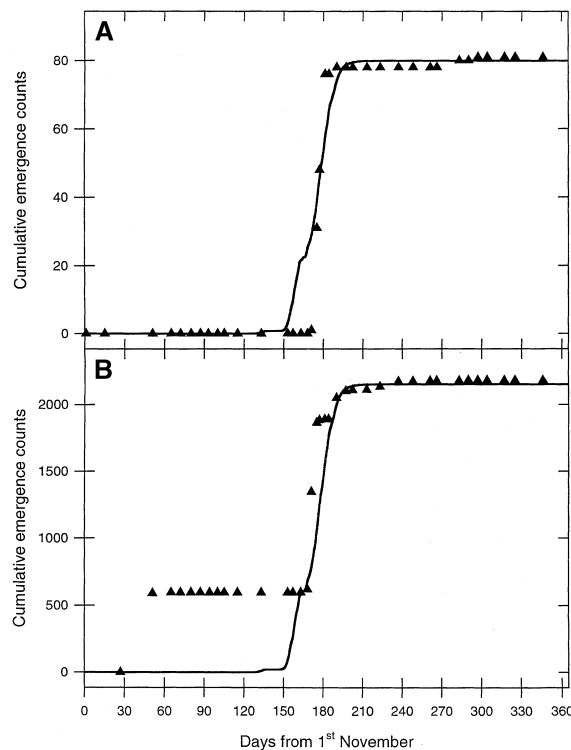


Fig. 8 Observed and predicted emergence timing for Danish local seed populations of *Stellaria media* between November 2000 and October 2001 inclusive. Cumulative emergence counts for local seed buried in Denmark: (A) in November 1999; (B) in November 2000; filled triangles, observed cumulative emergence counts; solid line, predicted cumulative emergence counts. Note different scales for cumulative emergence counts.

structure occurred from pot to pot at the same site during periods of dry summer weather. For some pots, the surface layer of peat was a stable disc with circular distance to the periphery, but other pots showed irregular cracks across the central parts of the top layer, thus facilitating light penetration into the sown layer. After the following period with rainfall in the autumn, most seedlings of *S. media* only emerged along the cracks, indicating that light penetration into soil is an additional key signal for germination (Tester & Morris, 1987; Kasperbauer & Hunt, 1988). A local variation in the surface structure of the sowing medium (peat) may well cause variable penetration of spurious amounts of light to induce locally variable germination of sensitized seeds that are well known to respond in terms of the very-low-fluence response of phytochrome A (Hartmann & Mollwo, 2000).

Ultimately, the development of robust models that are capable of predicting emergence for a wide range of environments and populations would be desirable. Despite some of the encouraging observations made in the present study suggesting potentially predictable synchrony in emergence, there are clearly further issues

that need to be addressed to test the theory rigorously. Substrate characterization and inclusion of additional soil types would improve wider application. Similarly, a wider range of weed populations combined with corresponding detailed understanding of the germination characteristics of those individual populations would help to quantify the between-population variation and identify repeating and potentially predictable patterns of behaviour. Such studies would help to explain the response of the seeds from different populations to chilling or define better experimentally the 'true' model parameters.

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